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Vol. 32 No. 10

BULLETIN

OF THE

TORREY BOTANICAL CLUB

OCTOBER, 1905

A new method of measuring the transpiration of plants in place*

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Very early in the history of the Desert Botanical Laboratory, it was recognized that the study of the transpiration of desert plants ought to be one of the leading lines of research. It was appreciated also that to be most effective the study should be confined as far as possible to plants growing under natural conditions, that is, to plants in the field.

That the task is not without its difficulties is readily seen. The forms of apparatus in general use are not intended and in fact are not well adapted for the determination of the transpiration of plants in place. It was necessary therefore in the very beginning to revise old methods, or to originate and to perfect a new one, both of which have been done.†

It is not to be understood that the method to be described, which was devised to meet the special need, is either ideal or has reached its final stage of development. But the use of it for a year in many experiments out-of-doors and under different conditions has shown it to be so practicable that a description of it at this time, together with some reference to experiments performed with it, appears to be desirable.

THE POLYMETER METHOD

Several methods are in general use by which the amount of watery vapor given off by plants may either be estimated, or

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* Papers from the Desert Botanical Laboratory of the Carnegie Institution, No. 5.

† This paper is devoted to the exposition of the method most used in 1904. Others are now being tried; should any of these appear to be satisfactory they will be described at another time.

[The BULLETIN for September (32 : 451–514) was issued 21 S 1905.]

demonstrated. These methods may be grouped into three classes. In the first of these the plant is potted, and weighed at intervals; the loss of weight is assumed to be due to the evaporation of water from its surface. In a second class the plant is enclosed in a tight receptacle and the vapor evolved from it is collected in some kind of drying material which is weighed before and after the experiment; any increase in weight is attributed to the absorption of water which was derived from the plant. In the third class the amount of water transpired is estimated from the amount absorbed by the plant. The apparatus employed in this class is some form of potometer.

The mere demonstration of the fact of transpiration has been made by placing the plant, or a portion of it, in a tight receptacle which encloses at the same time some hygroscopic material. The increase in the amount of vapor in the receptacle, or the presence of any considerable amount, is indicated by some visible change, as in the color or position, taking place in the substance.*

The method most used the past season at the Desert Botanical Laboratory is in principle a departure from any given above. It consists essentially in the determination of changes in the absolute humidity of the atmosphere in which the plant is placed; the difference in the absolute humidity, expressed in fractions of a gram, is the amount of vapor transpired. The calculations by which the absolute humidity is derived are based on variations of the relative humidity.

AN ACCOUNT OF THE APPARATUS

The form of apparatus with which, as was mentioned above, the most of the transpiration studies in the field were carried on during the past season at the Desert Botanical Laboratory was suggested early in 1904 by Dr. D. T. MacDougal of the Advisory Board of the laboratory. This is the apparatus used in the polymeter method for the determination of transpiration (see FIGURE 1).

The apparatus consists of a hygrometer, a bell-glass and a water-proof base. The form of hygrometer used was Lambrecht's *Reise* Polymeter. This instrument is especially constructed to record a variety of meteorological conditions; it is, however, well adapted to this other use. It is a substantially made brass instrument which carries a hair hygrometer and a thermometer, and is provided with a solid base which enables the instrument to stand upright when in use. The hygrometer indicates the relative humidity, and it is also provided with a scale by which the temper-

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* For a more detailed account of the methods used in studying the transpiration of plants, see BURGERSTEIN, Die Transpiration der Pflanzen, 1904.

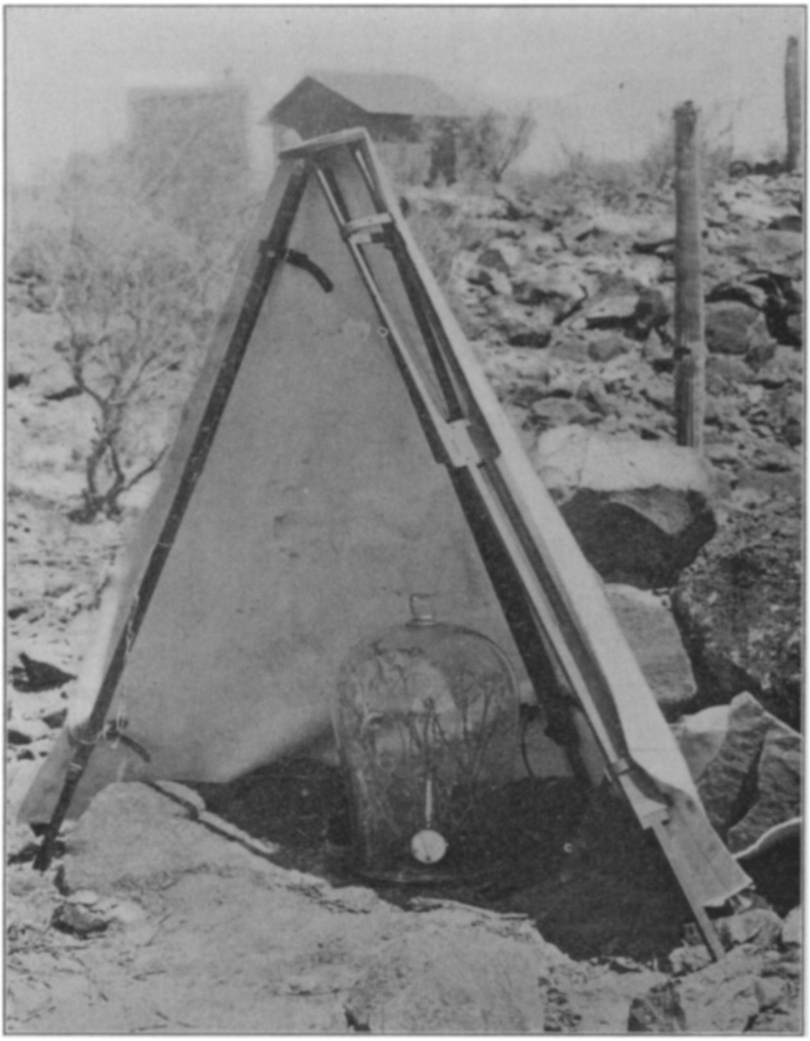

FIGURE I. Apparatus for determining the transpiration of plants in place. The polymeter method.

ature of the dew-point may be approximately determined. The maximum vapor-pressure for any temperature is written on the thermometer, which unfortunately is graduated according to the Fahrenheit scale. This instrument provides a means of telling directly, therefore, the temperature of the air, the maximum vapor-pressure, the relative humidity, and the dew-point. From what has been said regarding the polymeter it will appear at once that it can be used to demonstrate the fact of transpiration, and if the cubic contents of the bell-glass are known, from data given by it the amount of transpiration can also be estimated.

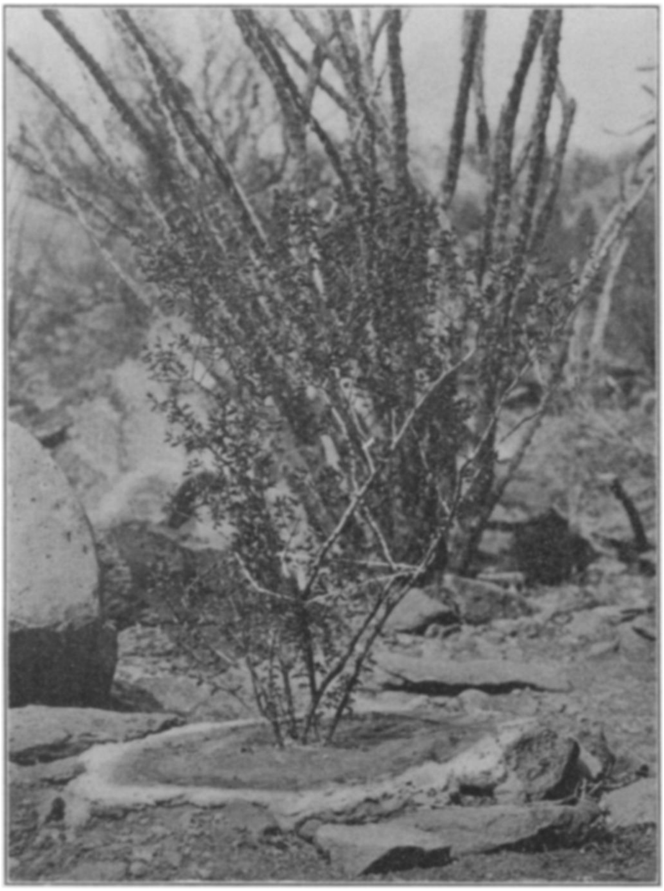

FIGURE 2. *Covillea tridentata*, showing base made of cement which was made water-proof by being covered by a mixture of vaseline and wax.

Any bell-glass which is adapted in form and in size to the plant, or branch, experimented with may be employed. Perhaps the best shape for general use is that of the bell shown in FIGURE 1, the enlarged upper portion of which permits the natural spreading of the plant. The size of the bell is of much importance, since it must correspond with the rate of transpiration. It can only be told by experience.

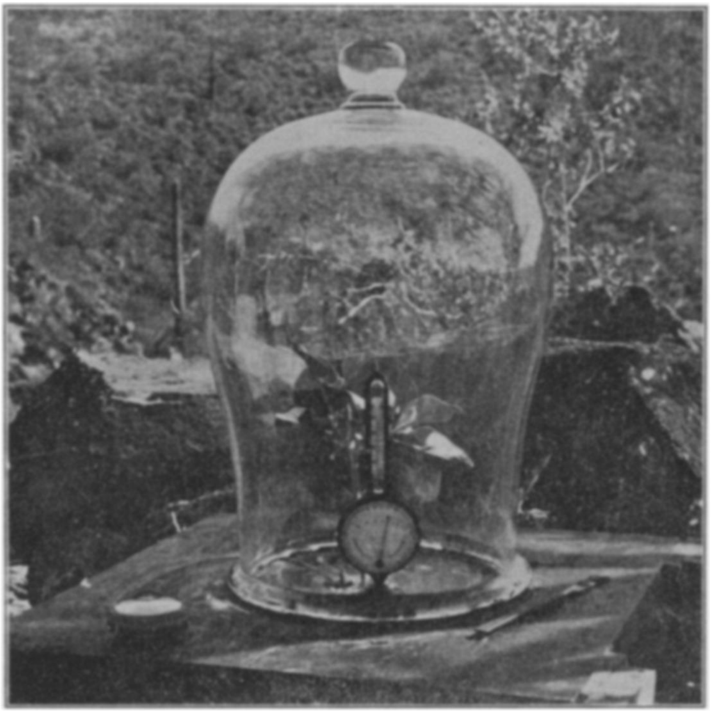

FIGURE 3. *Encelia farinosa*, with base constructed of wood. The base is made of two boards of which the one to the left is securely fastened to two cleats, which carry buttresses on the free ends, and the one to the right is clamped into position by interposing two wedges between the buttresses and the loose board. By removing the wedges the base is easily taken apart.

Finally, a base upon which to set the bell-glass and the polymeter must also be provided. The form may vary according to the nature of the experiment. If an entire plant is under observation, a cement base may be used (FIGURE 2). But this form, which was originally devised to be in a measure permanent, is not altogether satisfactory. A very good base for general use can be made of wood, like the one shown in FIGURE 3, for example, and it can be made so that it can be put together or taken apart quickly and with ease. Another form, shown in FIGURE 4, is made of an ordinary plant drier, which like the other forms of base described has been made water-proof by the application of vaseline or some other water-resisting substance. It sometimes happens that it is impossible or extremely inconvenient to use any of the bases above described. I have, for instance, carried the transpiration apparatus,

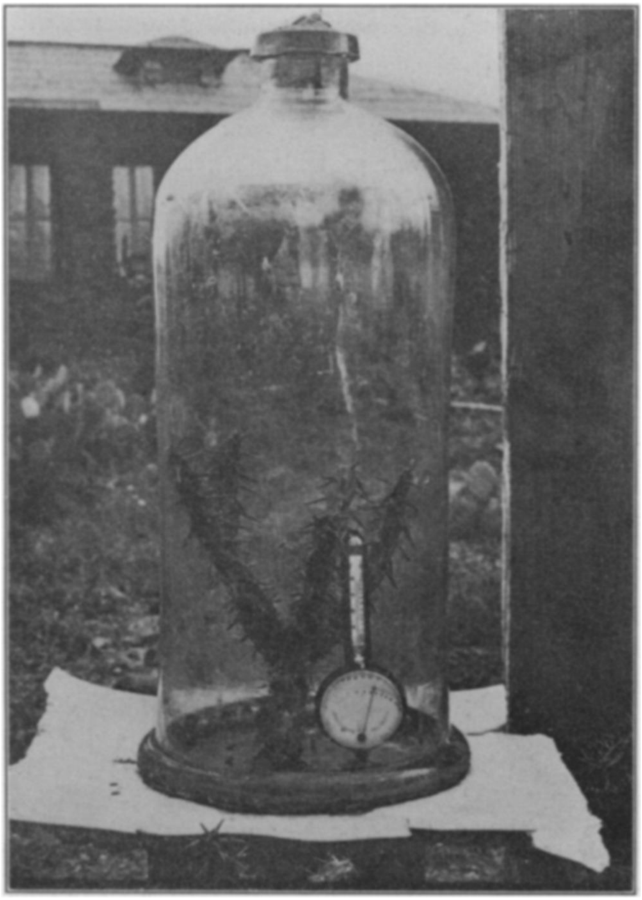

FIGURE 4. Method of observing the transpiration of a branch while still attached to the main plant. The plant is *Opuntia versicolor*.

packed on the back of a horse, for some miles into the mountains when it was necessary to make the load the lighest possible. In such a case oiled cloth of some sort was substituted with success for the heavier and more cumbersome forms of base. A cloth

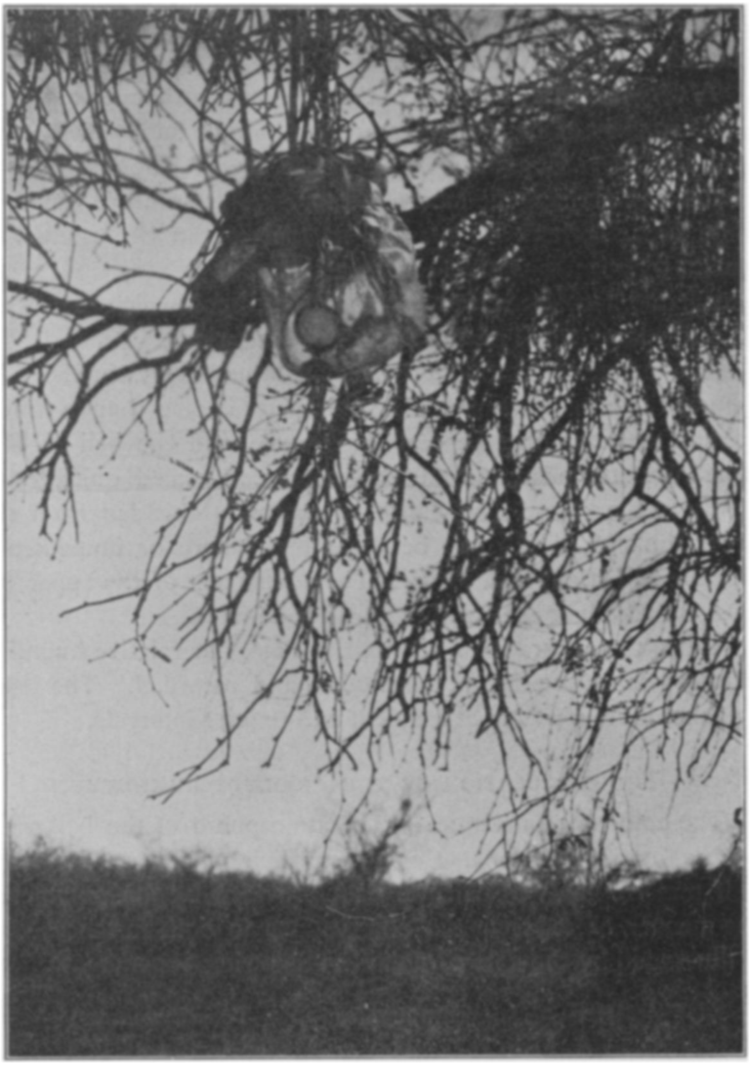

FIGURE 5. The manner of using the polymeter method in studying the transpiration of a mistletoe, *Phoradendron californicum.*

base is also frequently more convenient when studying the transpiration of such a plant as the mistletoe (FIGURE 5), or a branch of a tree. Whatever may be the style of base used, great care must be taken to avoid any leakage which would render the results quite untrustworthy.

A very necessary addition to the apparatus as above presented, in this country of high temperatures and bright sunlight, is some form of shade. Several types have been used. The one given in FIGURE 1 is perhaps the most satisfactory. It is made of heavy white duck. Straps are attached so that it can be fastened to camera tripods; it is thus easily carried and is very rigid when spread, and flaps are sewed to the bottom, upon which stones are piled to ensure a safe anchorage against the winds.

The manner of setting up the apparatus is very simple. As soon as the base is arranged, the polymeter is placed upon it in a position where it may be readily observed, and the bell-glass is placed over the plant and the polymeter and sealed quickly and tightly to the base. The entire apparatus is shielded from the direct sunlight, which can be done just before or immediately after the bell is put in position. The adjustment of the apparatus need not take longer than three or four minutes.

When the apparatus is set up, the time, the relative humidity and the temperature are at once taken and recorded. The readings should be repeated at frequent and regular intervals.

THE CALCULATION OF THE ABSOLUTE HUMIDITY

The amount of moisture in the atmosphere of the bell-glass may be found by a simple calculation, which may be based wholly, or if preferred only in part, on data provided by the polymeter. The manner of reducing the observations in both instances may be illustrated by the data given in the following experiment:

Time	Relative humidity	Temperature
9:33 A. M.	23	29° C. (84.2° F.)
10:00 "	50	The same

The bell has a capacity of 17,500 c.c.

A method of deriving the absolute humidity with the aid of data given entirely by the polymeter will be given first.

The polymeter gives 30 mm. as the maximum vapor-pressure at 84° F., and this number, 30, expresses also the weight in grams of one cubic meter of water-vapor at that temperature, since for the temperatures that usually occur the vapor-pressure in millimeters is expressed by almost the same number that gives the weight of water-vapor per cubic meter in grams.* That is, a cubic meter of saturated air, at sea-level, and at a temperature of 84° F., weighs (according to the polymeter) 30 grams.† At a saturation of 23 per cent. there would be 6.9 grams in one cubic meter (0.23 × 30). Multiplying this number by that fraction of a cubic meter which the capacity of the bell-glass represents, 0.0175 (17,500/1,000,000), gives 120 milligrams. Therefore, at a temperature of 84° F. and at a saturation of 23 per cent., the meteorological conditions at the beginning of the experiment, there were 120 milligrams of moisture in suspension in 0.0175 of a cubic meter, or in other words in the bell-glass.

If the second reading of the experiment is reduced in like manner it will give 262 milligrams as the amount of moisture which was in the bell-glass at 10:00 o'clock. The difference between 262 and 120 milligrams is the increase in the absolute humidity which is due to the transpiration of the plant. That is, 142 milligrams of watery vapor were given off by the plant in 27 minutes, and from this result the rate for any period and for any surface-area can be easily estimated.

The preceding method of deducing the amount of moisture from readings given by the polymeter is sufficiently accurate for tests, for purposes of demonstration, or for comparison, but is subject to certain very obvious errors. In the first place the vapor-pressure given by the polymeter is not so accurate as that provided by reliable hygrometric tables;‡ it cannot be read so closely. And, also, the maximum pressure of vapor in millimeters is not expressed at all temperatures that occur outdoors, at any rate in the desert region, by the number that gives the weight of vapor in grams per cubic meter. For example, the thermometer in summer not infrequently registers 95° F. (35° C.) in the shade, and often much higher. The weight of a cubic meter of saturated air at 35° C. is 39.187 grams; the maximum vapor-pressure at that temperature is, however, 41.78 mm.* I have, therefore, used the hygrometric tables in making all calculations.

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* HANN, Handbook of Climatology. English translation by R. DeWard, 1903.

† The number on the polymeter is really slightly less at the temperature, but as the scale is so small it cannot well be read more closely.

‡ Smithsonian Meteorological Tables, 1897, have been used in most of the reductions.

If, now, the absolute humidity is found for the above experiment by employing the hygrometric tables we shall get slightly different results.

The weight of one cubic meter of aqueous vapor at 29° C., and at sea-level, is given as 28.450 grams.† With a relative humidity of 23 per cent. the weight would be 6.54 grams for one cubic meter. Multiplying this by the fraction 0.0175, as before, gives 114 milligrams for the first reading. The second amount reduced in the same manner is 248.8 milligrams. Therefore the total transpiration, according to the latter method of making the computation, is 134.8 milligrams as against 142 by the first method, and this difference becomes greater with the rise of the temperature, since, among other reasons given above, the first method was based upon the pressure of vapor and not on its weight.

It has been mentioned above that the hygrometric tables are computed for sea-level. For delicate hygrometric work, therefore, some correction should be made for the higher altitudes, but for the usual work of estimating the transpiration of plants, partly because it is largely a comparison, slight altitudes above the sea need not be considered. Neither is it necessary to take into account the usual daily variation of the barometer. When on account of a considerable altitude above the sea, as at the Desert Botanical Laboratory (altitude 2,600 feet), it is necessary to take into account the diminished air-pressure, the final deductions for absolute humidity are multiplied by the following fraction:

$$\frac{\text{Gravity at altitude of experiment}}{\text{Gravity at sea-level}}.$$

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* Smithsonian Meteorological Tables, 1897, pages 133 and 142.

† *L. c.*, page 133.

TESTING THE POLYMETER METHOD

Laboratory experiments for the purpose of testing the accuracy of the method indicate that the polymeter used for the present object generally registers too low. This is due to the slow diffusion of moisture in a confined space as well as to a tardy reaction of the instrument itself. But these experiments show, on the other hand, the very important fact that when the instrument is handled properly, in a uniform manner, it will give results which are consistent.

The succeeding experiments, which were conducted in the laboratory in a manner to be detailed, give some idea of the behavior of the instrument in regard to the rate of increase or decrease of moisture in the bell-glass.

EXPERIMENT NO. 1.—*Reaction of the polymeter to a change in the relative humidity which is approximately one per cent. a minute.* The apparatus was arranged in the following manner: A bell-glass was placed over a polymeter and sealed to a ground-glass plate. Inlet and outlet tubes were arranged so that the amount of moisture in the bell could be increased or diminished at pleasure. At the beginning of the test the humidity of the atmosphere of the bell-glass was increased to a certain per cent., which was indicated by the polymeter, after which a portion of it was withdrawn and collected in sulphuric acid drying-tubes. The polymeter was again read. The amount of vapor which was taken away from the bell-glass was then computed by the hygrometric method as given in the preceding pages, and it was compared with the amount as determined by the increase in the weight of the drying tubes. According to the polymeter the vapor removed was 88 mg.; the tubes gained 90 mg. in weight. Thirty-seven minutes were taken to remove the moisture from the bell-glass, during which the polymeter recorded a decrease of 33.5 per cent. in the relative humidity.

EXPERIMENT NO. 2.—*Reaction of the polymeter to a variable change in the relative humidity.* The apparatus was set up as before. Calcium chloride drying-tubes were used. A stream of moist air was passed through the bell-glass from 10:41 until 10:47, when all openings were again closed.

The following data were recorded:

Time	Relative humidity	Temperature
10:41	43	74° F.
10:47	61	74
11:10	63	74

It will be observed that the humidity increased 18 per cent. in 6 minutes (10:41–10:47). From 10:47 to 11:10 the instrument was allowed to settle, during which time it showed an increase of 2 per cent. This was due to the tardy response of the polymeter, since the moisture was equally distributed throughout the bell-glass by reason of the manner of introducing it.

At 11:10 the stream of moist air was again sent through the bell-glass; it was stopped at 11:17.

11:17	68	74
11:37	67	75

The rise of 5 per cent. of the humidity in 7 minutes (11:10–11:17) was closely followed by the polymeter, since it showed no change except only a fall of one per cent. due to the higher temperature, in the succeeding period of rest.

At 11:37 a portion of the moisture was removed from the bell-glass and collected in calcium chloride drying-tubes. This process required 12 minutes, during which the humidity fell 25 per cent.

11:49	42	75.5

According to calculations based upon the polymeter, the amount of moisture withdrawn was 42 mg.; the drying-tubes gained 55 mg. That is to say, the polymeter, on account of the too rapid decrease in the humidity, lagged considerably in its recording.

BEST METHODS OF CONDUCTING THE EXPERIMENTS

When an experiment is performed it is necessary to compromise between the desirability of making it as short as possible, in order to maintain conditions for the plant as nearly normal as practicable, and the fact that the instrument, for reasons given above, does not record instantly the humidity of the air. Consequently the rate of increase in the relative humidity should be as nearly constant for all experiments as possible, particularly when comparative studies are carried on, and it should not be over 1 per cent. a minute. This condition is fairly well attained by varying the size of the bell-glass in accordance with the rate of transpiration. It can be told only by trial.

Although the relative humidity of the atmosphere of the bell-glass cannot be lowered to suit the convenience of the operator, without subjecting the plant to grossly unnatural conditions even on the desert, it is altogether best if at the beginning it does not greatly exceed 25 per cent. The experiment can then be so conducted that a considerable range in the relative humidity is possible without greatly modifying the moisture conditions; the range need not be greater, if so ample, as that to which the plant is daily subjected in the open. If this precaution is taken the decrease in the rate of transpiration which accompanies an increase in the humidity can largely be avoided.

The foliage should be uniformly distributed throughout the bell-glass so that the diffusion of the watery vapor may be as quickly attained as possible. This may be facilitated by the use of some device by which the circulation of the air may be maintained.

The temperature can be kept fairly uniform if the apparatus is allowed to become of the same temperature as the plant and the base, provided a permanent base is used, but in case the day is unusually hot and a large increase in heat is observed, notwithstanding the shade, a dampened blotter or cloth tied to the outside of the bell-glass and large enough to cover one-third of its surface, will in a very satisfactory manner keep the temperature down.

SUMMARY AND CONCLUSIONS

The polymeter method has been in use one year, during which time about 100 experiments were performed with it. All of these, with the exception of a single series, were conducted upon plants in place, and the experiments, an account of which will be given at another time, showed very conclusively that the new method is a practicable one for outdoor use. The following summary is given, with sufficient illustrations drawn from the work of the year to give some conception of the scope of the method and more especially of its efficiency.

1. The polymeter method of determining the transpiration of plants is based upon changes in the relative humidity of the atmosphere in which the plants are placed. From data respecting the relative humidity and the temperature, provided by the polymeter, the absolute humidity is calculated by well-known methods. The difference in the absolute humidity constitutes the amount transpired.

2. The results derived from the use of the method are shown by laboratory tests to be consistent, and, provided certain precautions are taken, to be reasonably accurate.

3. The apparatus is easily adjusted, it is not likely to get out of order, and it may be easily transported.

4. The new method is especially suitable for use in a dry locality; where the humidity is high some other method will probably be more satisfactory.

5. That the range of the use of the method outdoors is large will be perceived by the following list which is a part only of the plants studied: *Cereus giganteus*, *Covillea tridentata*, *Encelia farinosa*, *Fouquieria splendens*, *Fraxinus arizonica*, *Phoradendron macrophyllum*, *Pinus ponderosa*, *Quercus oblongifolia*, *Kallstroemia maxima*, and *Verbena ciliata.*

6. It will be observed by the list that not only entire plants in place, but also portions of plants while still attached, can be employed. This greatly enhances the usefulness of the method, as the following indicates: In a certain experiment on a mistletoe and its host, the transpiration of the mistletoe was taken while it was still growing on its host and then the apparatus was readjusted and the rate of the host branch upon which the mistletoe grew was observed. When these experiments were completed the transpiration of a seedling of the same species as the host plant was learned. Thus results of much pathological and physiological importance were surely and readily obtained.

7. It is important to note that a plant can be experimented upon repeatedly without apparent injury, which makes it possible to observe the transpiration at hourly or at daily intervals, and thus to learn the diurnal or the seasonal variations as desirable. As a single instance of seasonal differences in rate, the transpiration of *Fouquieria* may be cited. The absolute seasonal variation

in rate of this plant was 8.03 milligrams per minute for 100 sq. cm. of transpiring surface. The least rate was that of March when 0.22 milligrams for the same area and period was observed, and the highest was in August when the rate was 8.25 milligrams.

8. The apparatus is so sensitive to changes in the humidity — to give an illustration of the delicacy of the method — that it was possible to demonstrate and to estimate the transpiration of *Echinocactus* during the extremely hot and dry climatic conditions of June, at a time when the transpiration of all desert plants was very feeble. It is of interest to observe that the cobalt nitrate method as employed to demonstrate transpiration was quite ineffective as a means of showing any transpiration of the plant.

9. Finally the convenience with which the apparatus may be transported may be mentioned. This feature makes it possible to extend the work into out-of-the-way places, as for example, to study the effects of altitude on the rate of transpiration when the experiments have to be carried on in the mountains. As a single instance of this use of the method the following may be given: Some experiments on *Helenium Hoopesii* were performed at different altitudes in the Catalina Mountains, which are not far distant from the laboratory but which are rough and rather difficult to enter. A portion of the experiments were conducted at an altitude of 7,600 feet and a portion at an altitude of 9,150 feet. The general result of these studies may be summed up by the statement that they tended to support the view that the altitude directly affects the rate of transpiration, which in the present case was greater at the higher altitude.

DESERT BOTANICAL LABORATORY OF THE
CARNEGIE INSTITUTION.